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# Density-dependent recruitment rates in great tits: the importance of being heavier

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In birds, individuals with a higher mass at fledging have a higher probability of recruiting into the breeding population. This can be because mass is an indicator of general condition and thereby of the ability to survive adverse circumstances, and/or because fledging mass is positively related to competitive strength in interactions with other fledglings. This latter explanation leads to two testable predictions: (i) there is stronger selection for fledging mass when there is more severe competition (i.e. at higher densities); and (ii) that besides absolute fledging mass, relative mass of fledglings within a cohort is important. We test these two predictions in two great tit (*Parus major*) populations. The first prediction was met for one of the populations, showing that competition affects the importance of mass-dependent recruitment. The second prediction, that fledglings recruit relatively well if they are heavy compared to the other fledglings, is met for both populations. The consequence of the importance of relative rather than absolute fledging mass is that the fitness consequences of reproductive decisions affecting fledging mass, such as clutch size, depend on the decisions of other individuals in the population.

**Keywords:** *Parus major*; density dependence; selection; body mass; fledging mass; recruitment

## 1. INTRODUCTION

The trade-off between quality and quantity of offspring is one of the central themes in life-history theory (Lessells 1991; Stearns 1992; Daan & Tinbergen 1997). The theory on clutch size optimization includes both this trade-off and the trade-off between current and future reproduction (Charnov & Krebs 1974). In birds, parents can increase recruitment of their offspring by raising heavy chicks (Perrins 1965; Tinbergen & Boerlijst 1990; Magrath 1991; Lindén *et al.* 1992; Verboven & Visser 1998). Tinbergen & Boerlijst (1990) showed that the recruitment rate of chicks is causally affected by their mass, but the mechanism behind this process is still poorly understood. The two non-mutually exclusive alternatives are that mass reflects a general condition measure, affecting survival during adverse circumstances (Perrins 1965; Garnett 1981) or that mass is an indicator of competitive strength in interactions with other juveniles in the population. Garnett (1981) indeed showed that heavy offspring have more fat, but also showed that they were structurally bigger. The fat store is only enough to last, at the most, one day of starvation (Garnett 1981), which makes it unlikely that this is the most important explanation for the better recruitment rate of heavier fledglings (see Saino *et al.* 1997). The alternative is that a correlation exists between competitive strength and mass, which enables heavier offspring to survive better. This hypothesis is supported by the observed positive association between the proportion of fights won and

the size of fledgling great tits (Garnett 1981). Sandell & Smith (1991) showed that juvenile males were only able to defeat adult males if they were bigger. If mass is indeed important in competition, it is expected that mass relative to the mass of the other fledglings in the population is the important factor.

The strength of selection should depend on the competitor density, although few examples are available in natural circumstances (see Moorcroft *et al.* 1996). Individual reproductive decisions might depend on the competitive environments juveniles face after independence. Density dependence of clutch size in birds has been proposed to be such an adjustment to expected competition levels (Krebs & Perrins 1978), because reducing clutch size results in higher-quality offspring. In years with high densities, competition between juveniles will be severe, and only the heaviest offspring will survive. In years with low densities, mass might be less important and parents can maximize their fitness by producing more, but lighter offspring. Thus, even in the absence of competition in the egg-laying or chick-feeding stage, this process can explain why clutch size often decreases with increasing density (see Sinclair (1989) for a review). If this process occurs we expect that (i) selection for heavy offspring is positively related to density, and (ii) the recruitment rate of offspring is affected by their mass relative to the mass of other fledglings. The relative mass would be more important in high-density years because of the stronger competition in those years (see Kluyver 1971; Tinbergen *et al.* 1985; Verhulst 1992). If the fitness associated with a certain mass indeed depends on the mass of competitors in the population, the parental decisions on clutch size which affect the fledging mass can only be optimized if decisions of other pairs in the

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population are taken into account. Clutch size optimization should in this context be treated as a game theoretical problem (Maynard Smith 1982) rather than as simple optimization. In this paper we test the two predictions outlined above using data from two great tits populations on which long-term studies have been carried out at the Netherlands Institute of Ecology.

## 2. METHODS

Data are presented from great tit populations in the Hoge Veluwe and Vlieland (The Netherlands). Tinbergen and Boerlijst (1990) gave detailed descriptions of the study areas and standard procedures. Data from 1975–1995 were used for the Hoge Veluwe area (excluding 1980–1982 when fledglings were not weighed). Data from the 1979–1995 were used for the Vlieland population (excluding 1984). All nest-boxes were checked weekly, and all chicks were ringed in the nest and weighed 14–16 days after the hatching of the first chick in the brood. This mass is the asymptotic nestling mass and is further referred to as fledgling mass (van Balen 1973). The relative mass is the difference between the mass of the individual and the annual mean mass, divided by the standard deviation of mass in that year. Fledglings were recorded as having recruited to the breeding population if they were caught as breeding adults in the same area in subsequent years. Recruitment rate is the number of recruits divided by the number of fledglings. No correction has been made for capture probability, because in our populations the capture probability is high (92% for females and 73% for males; Bauchau & Van Noordwijk 1995) and capture probability of recruits is independent of fledgling mass (Verboven & Visser 1998). Recruitment is the product of the survival probability, and the probability of getting a territory and breeding for those individuals that have survived. Territory defence starts in autumn (Drent 1983), and from that moment the juveniles compete for space with both adults that bred in the previous breeding season, and other juveniles that are attempting to establish a territory. The probability of territory establishment is negatively related to adult density at the time of territory settlement, and possibly positively related to juvenile density (Tinbergen *et al.* 1987). The latter might be an effect of adults having more problems in defending their former territory against a larger number of juveniles. Thus, although competition is among juveniles, the extent of competition is probably set by the density of adults. We therefore used the number of breeding pairs per hectare as a measurement of density. Throughout this paper we only used first brood fledglings in the analysis because second brood fledglings are subordinate to first brood fledglings (Drent 1983) and, as a result, their recruitment is strongly affected by the density of first brood fledglings (Kluyver 1971; Tinbergen *et al.* 1985; Verhulst 1992).

Male fledglings are on average 1 g heavier than female fledglings in these populations. Although dominance is related to sex, with males being more dominant than females, we did not take sex into account in the analysis. The practical reasons for this are that only a proportion of the fledglings had been sexed, and that the accuracy of sexing depends on mass (Verboven & Visser 1998). The fact that competition also occurs between the sexes provides a reason to analyse the two sexes in a single analysis.

### (a) Tests of the predictions

To test the first prediction—that selection for heavy fledglings is positively related to density—we quantified selection for

fledgling mass using standardized selection differentials. The standardized selection differential for fledgling mass is defined as the difference between the mean mass of the fledglings that recruit and the mass of all fledglings in that year divided by the standard deviation of fledgling mass of all fledglings in that year (Falconer 1981). We then used a Spearman's rank correlation to test whether the standardized selection differential and density of adults in the year of fledging are positively correlated.

This analysis has one drawback: a positive correlation will also be found when fledglings of a certain mass have a fixed (i.e. not density dependent) probability of recruiting and when the mean mass of all fledglings is negatively related to density. To explore this possibility we calculated the correlation between the annual mean fledgling mass and density.

To test the second prediction—that the recruitment rate is affected by the relative fledgling mass—we grouped the fledglings into 1 g mass classes. For each of these mass groups we calculated the recruitment rate. To correct for the large differences in mean annual recruitment rate (due to environmental factors and density-dependent recruitment rates; Perrins 1965; Tinbergen *et al.* 1985) these recruitment rates of different mass groups were divided by the annual recruitment rate of all fledglings. To obtain relative fledgling mass we standardized the mass of a group by subtracting it from the mean annual fledgling mass and dividing it by the standard deviation. We then calculated the correlation between the relative recruitment rate and the relative fledgling mass for all mass groups. We predicted a positive relationship, but not over the entire range of fledgling masses. Fledglings that are in the upper group will be the heaviest fledglings in all years and are not expected to be affected by the distribution in mass of the other fledglings in the population. The same rationale holds for the lightest fledglings. If relative mass is important we expected that the strongest effect in groups with intermediate mass, because these are relatively light in some year while relatively heavy in others.

There is also a pitfall in this analysis. If a correlation between the mean annual recruitment rate and mean annual fledgling mass was found, then using relative recruitment rate and relative mass would automatically lead to a positive correlation, even if recruitment is only dependent on absolute mass. However, V. Perdeck, M. E. Visser, J. H. van Balen and N. Verboven (unpublished data) showed that mean recruitment rate is not correlated to mean fledgling mass for both great tit populations (Hoge Veluwe:  $r_s = 0.14$ ,  $n = 16$ ,  $p = 0.61$ ; Vlieland:  $r_s = -0.09$ ,  $n = 15$ ,  $p = 0.75$ ).

## 3. RESULTS

The standardized selection differential for fledgling mass was positive in both populations (mean  $\pm$  s.d. for Hoge Veluwe =  $0.29 (\pm 0.19)$  s.d. units, for Vlieland =  $0.24 (\pm 0.12)$  s.d. units). It was positively associated with density for the Hoge Veluwe populations, but not for those from Vlieland (figure 1). The difference between the areas in the effect of density on the selection differential was confirmed in a two-way ANCOVA where the slopes differed between the areas (interaction area  $\times$  density:  $F_{1,29} = 7.00$ ,  $p = 0.013$ ).

For the Hoge Veluwe populations this was not because mean fledgling mass of all young correlated negatively with the density, although there appeared to be a negative trend ( $r_s = -0.34$ ,  $n = 18$ ,  $p = 0.17$ ). In the Hoge Veluwe area the mean mass of the fledglings that

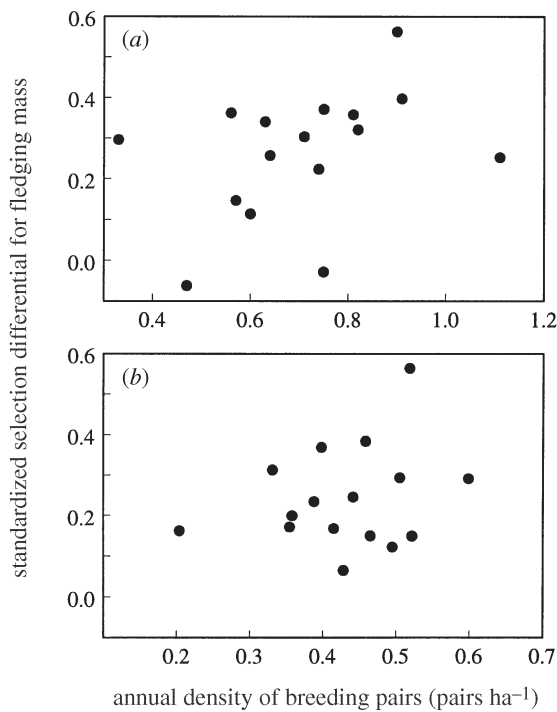


Figure 1. The annual standardized selection differential for fledging mass plotted against the annual density of breeding pairs. (a) Hoge Veluwe ( $r_s = 0.49$ ,  $n = 17$  and  $p = 0.046$ ) and (b) Vlieland ( $r_s = 0.05$ ,  $n = 16$  and  $p = 0.85$ ).

recruited into the population was also not correlated with the density ( $r_s = -0.018$ ,  $n = 18$ ,  $p = 0.47$ ). The partial correlation between selection differential and density after correcting for the average fledging mass still approached significance ( $r_s = 0.45$ ,  $n = 17$ ,  $p = 0.07$ ), suggesting that the effect of density on selection was not only due to the average fledging being of lower mass. For Vlieland, both the mass of all the fledglings ( $r_s = 0.57$ ,  $n = 16$ ,  $p = 0.022$ ) and the fledging mass of those birds that recruit ( $r_s = 0.65$ ,  $n = 16$ ,  $p = 0.0064$ ) were significantly positively correlated with density. The partial correlation between the selection differential for fledging mass and density after correcting for the annual mean fledging mass was positive, but still not significant ( $r_s = 0.35$ ,  $n = 16$ ,  $p = 0.18$ ). The increase in fledging mass with density on Vlieland could be caused by parents decreasing their clutch size in response to density, to produce heavier offspring in years of high competition. If this is so, we expect an effect of density on clutch size, as well as a correlation between clutch size and fledging mass. The annual fledging mass was positively correlated with the annual mean clutch size for the Hoge Veluwe area ( $r_s = 0.72$ ,  $n = 17$ ,  $p = 0.001$ ), but not for Vlieland ( $r_s = -0.049$ ,  $n = 16$ ,  $p = 0.85$ ). The annual mean clutch size correlated negatively with the annual density for the Hoge Veluwe area ( $r_s = -0.80$ ,  $n = 17$ ,  $p = 0.0001$ ), but not significantly so for Vlieland ( $r_s = -0.38$ ,  $n = 16$ ,  $p = 0.15$ ; although in a larger data set the effect was significant, see Both (1998)). Thus, in the Hoge Veluwe area, in high-density years the birds raised both fewer and lighter offspring. In Vlieland, clutch size was not statistically significantly affected by density and, thus, the increase in fledging mass with density could not be

shown to be due the density-dependent reduction in clutch size.

Relative survival correlated positively with relative fledging mass for 19 g fledglings in Hoge Veluwe, and for 17 g fledglings in Vlieland (table 1, figure 2). In both cases the group recruited relatively badly if they were lighter than the other fledglings in the population, while they recruited well if they were relatively heavy. As predicted, the trend between relative recruitment rate and relative mass was not found for the lower and upper part of the mass distribution (table 1). In Vlieland the trend was found in the group that was 2 g lighter than in Hoge Veluwe, which could be partly attributed to the lower average fledging mass in Vlieland (mean  $\pm$  s.d.  $16.7 \pm 1.9$  g) compared with Hoge Veluwe ( $17.2 \pm 1.9$  g).

#### 4. DISCUSSION

In one of the populations, there was stronger selection on fledging mass when the density was high. This was not due to a clear pattern of fledging mass decreasing with density, nor to the average fledging mass of recruits increasing with density. In both populations there was a group of fledglings of intermediate mass that recruited relatively badly when they were relatively light and relatively well when they were relatively heavy. Since the annual recruitment rate was not correlated with the annual mean fledging mass, this indicates that, within a certain range, recruitment of fledglings also depends on their relative mass instead of only their absolute mass.

The relationship between the selection for mass and density clearly differed between the populations. The reason for the lack of an effect of density in Vlieland might be due to a steady increase in population size over the study, probably because of forest maturation. This means that, over the study period, breeding density is not a good indicator of the competitive pressure that individuals experienced. If the residual densities to the year trend are taken instead as an estimate of the competitive pressure, the correlation coefficient between selection for mass and the residual mass for Vlieland becomes positive, although not significantly so ( $r_s = 0.21$ ,  $n = 16$ ,  $p = 0.44$ ). In contrast, the Hoge Veluwe area consists of relatively mature forest and the great tit population did not increase or decrease over the study period. Using the residual instead of actual densities for this area did not alter the conclusions. Thus, the difference between the populations might be the result of using density as a measure of competition, without taking into account the long-term changes in the level of resources over which competition takes place.

Fledging mass as an indicator of competitive strength implies that it is not only important to have a certain mass, but also that it is important to be heavier than competitors. Our results corroborate this idea: fledglings of intermediate mass were more likely to recruit if they were relatively heavy in that year. This effect does not seem to be affected by heavier offspring fledging earlier in the season and therefore having a higher competitive value, as has been shown for song sparrows, *Melospiza melodia* (Arcese & Smith 1985). In great tits, recruitment was negatively related to the fledging date, but after correcting for date the fledging mass still had a strong effect on recruitment chances (Verboven & Visser 1998). Tinbergen and Boerlijst

Table 1: *Spearman's rank correlations across years between relative survival and relative mass for groups of equal mass*

( $n$  is the sample size in years. 'Recruitment' is the mean (s.d.) of the relative recruitment rates over all the years. Data were used only if there were more than 20 fledglings of a particular mass in a year. For Vlieland there were no data for the group  $>19.5$  g.)

mass (g)	Hoge Veluwe				Vlieland			
	$r_s$	$n$	$p$	recruitment	$r_s$	$n$	$p$	recruitment
15.5–16.5	0.39	18	0.110	0.89 (0.50)	0.19	15	0.49	0.98 (0.22)
16.5–17.5	0.14	18	0.590	1.02 (0.34)	0.70	15	0.004	1.12 (0.23)
17.5–18.5	0.28	18	0.260	1.30 (0.57)	0.14	15	0.62	1.23 (0.22)
18.5–19.5	0.51	17	0.036	1.42 (0.76)	0.01	14	0.97	1.26 (0.36)
$>19.5$	–0.15	11	0.650	1.48 (1.00)	—	0	—	—

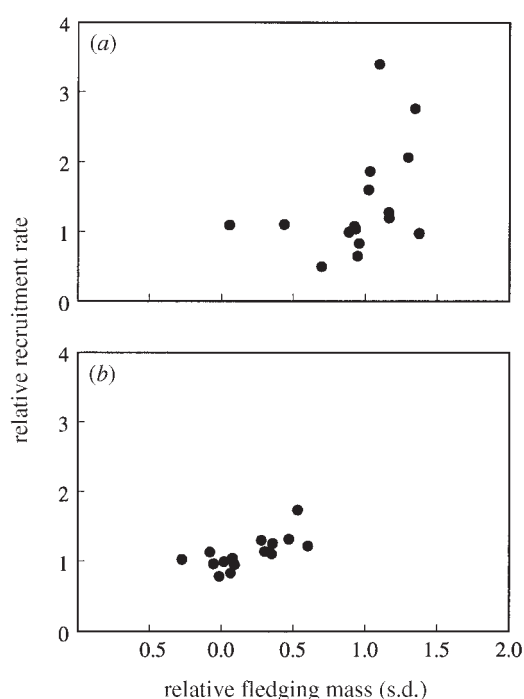


Figure 2. The relative annual recruitment rate of fledglings of a certain mass plotted against their relative mass in the population. The two figures are from the two groups in which a significant association was found (table 1). (a) Fledglings of 18.5–19.5 g in Hoge Veluwe and (b) fledglings of 16.5–17.5 g in Vlieland.

(1990) also showed that within broods the heavier fledglings recruited better than the lighter ones.

The consequences of the importance of relative mass are that the pay-off of strategies affecting mass are no longer independent of the strategies practised by other individuals (Maynard Smith 1982). The clearest example is clutch-size optimization (see Petersen & Hardy (1996) for a similar argument). Clutch size directly affects fledgling mass, but the fitness associated with fledgling mass and, thus, clutch size, is dependent on the mass distribution of the fledglings from the other broods in the population. Thus, parents should in principle also take the clutch sizes of their neighbours into account in deciding what clutch size to lay. Although this can result in runaway selection for smaller clutches and thus heavier offspring, this process is probably stopped because the product of the number and recruitment rate of offspring (i.e. the fitness of the current clutch) decreases. This depends on the shape of the relationship

between recruitment rate and relative mass. If the heaviest juveniles in the population always recruit and the recruitment rate is low, then we expect runaway selection. If absolute mass is important because of the survival value of fat reserves, or a large random effect exists on recruitment, in addition to the mass dependent component, then runaway selection is not likely.

If the relative mass indeed explains an important part of recruitment and hence fitness, this might affect the results of clutch-size manipulation studies in which a large proportion of the broods in a population were manipulated (e.g. Högstedt 1980; Pettifor *et al.* 1988; Tinbergen & Daan 1990). These manipulations not only altered the distribution of brood sizes, but also changed that of fledgling mass and, hence, the recruitment rates of chicks with particular masses. As this affects the measured fitness return of a manipulated brood such experiments can no longer be interpreted as the equivalent of a point mutation in an unchanged environment.

Density dependence of clutch size might be explained by the importance of relative mass on recruitment (Krebs & Perrins 1978). In years with high density, parents can respond adaptively to the expected high level of competition by producing fewer, but heavier, offspring. In the Hoge Veluwe population the annual mean clutch size declined with density (as was found for Vlieland in a larger data set, and in other populations of great tits; Both 1998), but mean fledgling mass was not positively correlated with density in either population. There is, however, the possibility that parents have less resources to invest in high-density years, because of increased competition before or during the nestling stage (Arcese & Smith 1988). If they do not reduce their clutch size they will raise even lighter chicks, so the observed reduction of clutch size might still function to allow parents to raise chicks of relatively high mass. Further reduction of clutch size might give the fledglings a higher survival value still, but it would not be sufficiently high to offset the decreases in the number of offspring.

The population consequences of relative mass-dependent recruitment are as yet unclear. This selection will reduce the number of fledglings and probably increase the competition between juveniles because of their greater competitive strength. The effect on population dynamics might, however, be slight, because of the strong density dependence of recruitment rates. We have, however, shown that for individual pairs it may pay to adjust brood size to the strength of competition juveniles face after leaving the nest. Considering clutch-size decisions in a game



theoretical framework can add important explanatory power to the study of the evolution of reproductive decisions.

Hans van Balen was most important in managing the project for many years in a standardized way. Jan Visser took care of the database, and he and Huibert van Eck were very important in doing the field work. Stichting 'Het Nationale Park De Hoge Veluwe' and Staatsbosbeheer Vlieland gave kind permission to work on their property. Ab Perdeck generously allowed us to use some of his unpublished work. The paper highly improved from comments on earlier drafts made by Kate Lessells, Arie van Noordwijk, Joost Tinbergen, and two anonymous referees. This is publication 24g4 of the NIOO Centre for Terrestrial Ecology, Heteren, The Netherlands.

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